Physica A 389 (2010) 3956–3964

Contents lists available at ScienceDirect

Physica A

journal homepage: www.elsevier.com/locate/physa

Mean field approximation for noisy delay coupled excitable neurons

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ARTICLE INFO

Article history:
Received 20 February 2010
Received in revised form 2 April 2010
Available online 4 June 2010

Keywords:
Time-delay
Stochastic excitable systems
Mean-field

ABSTRACT

Mean field approximation of a large collection of FitzHugh–Nagumo excitable neurons with noise and all-to-all coupling with explicit time-delays, modelled by $N \gg 1$ stochastic delay-differential equations is derived. The resulting approximation contains only two deterministic delay-differential equations but provides excellent predictions concerning the stability and bifurcations of the averaged global variables of the exact large system.

1. Introduction

Small parts of brain cortex may contain thousands of morphologically and functionally similar interconnected neurons. Realistic models of an individual neuron, like Hodgkin-Huxley, FitzHugh–Nagumo (FN) or Hindmarsh-Rose to mention only a few popular examples [1], are given by few-dimensional nonlinear differential equations. Transport of information between neurons can be phenomenologically described by time-delayed inter-neuronal interaction (please see Ref. [2] and the references therein). It is also well known that neurons *in vivo* function under influences of many sources of noise [3], and versatile effects of various types of noise on model neurons have been studied (see for example [4–7]. Considering all mentioned factors it is clear that a basic, relatively detailed mathematical model of a small part of realistic cortex should involve an extremely large system of nonlinear stochastic delay-differential equations (SDDE). Analyzes of such complex models is impossible without more or less severe approximations, which should be adopted to different purposes. It is our goal to study some aspects of an approximation by only two deterministic delay-differential equations (DDDE) of an example of a complex neuronal system described by many-component SDDE. We shall see that, although the approximate model is very simple, the predicted critical parameter values for the bifurcations and stability of the stationary states are in excellent quantitative agrement with those of the exact complex model within a relevant domain of parameters.

Neuronal dynamics with all three factors (large number of units, delayed interaction and noisy environment) included has been studied much less than the influence of each of the factors separately [8]. The important influence of noise alone on a single, small number or large clusters of neurons has been studied much in recent years [7]. It is also well known that time-delay can have important qualitative effects on the stability of stationary states (please see for example Refs. [2,9,10]) and synchronization of neuronal dynamics [11,12]. Studies of the combined effects of noise and time-delay have mostly, but not entirely [13] been restricted to artificial networks [14,15] or small numbers of neurons (usually two) [16,17]. An example of a study of a large collection of noisy realistic neurons with delayed coupling can be found in Ref. [13] (see also the references therein).

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0378-4371/$ – see front matter
doi:10.1016/j.physa.2010.05.048

The mean field approach (MFA) is based on a set of approximations that replace a many component system by a simpler system described by a small number of (averaged) collective or macroscopic properties. The mean field approximation has been applied to systems of excitable neurons with noise but with no time-delay for example in Refs. [18–20,7]. Otherwise a type of MFA was devised in Refs. [21,22] and applied to large clusters of noisy neurons with time-delayed interaction in Ref. [13]. However, the approximations made in these papers resulted in a system of equations that is still too large to be analyzed analytically, so that the approximate system must be studied numerically. We shall derive an approximate system of only two DDDE for the dynamics of the mean fields. Such a simple system allows analytical treatment of bifurcations and the parameter domains of stability of the stationary states which turn out to be in a quite good agreement with the exact complex system.

2. The model and its mean field approximation

We shall study a system of excitable neurons modelled by the following set of SDDE:

$$\epsilon \mathrm{d}x_i = f(x_i, y_i)\mathrm{d}t + \frac{c}{N}\sum_{j=1}^{N}(x_j(t-\tau) - x_i)\mathrm{d}t$$
$$\mathrm{d}y_i = g(x_i, y_i)\mathrm{d}t + \sqrt{2D}\mathrm{d}W_i \tag{1}$$

with

$$f(x, y) = x - x^3/3 - y + I$$
$$g(x, y) = x + b, \tag{2}$$

where b, I, c, D and $\epsilon \ll 1$ are parameters. The formulas (2) represent one of the common ways of writing the famous FitzHugh–Nagumo model [1] of excitable behavior. For certain parameter values, like $b = 1.05$, $I = 0$ to be used throughout this paper, the ODE given by (2) have a stable stationary solution (x_0, y_0) such that small departures from (x_0, y_0) might lead to large and long lasting excursions away from (x_0, y_0) which nevertheless end up on the stable state (x_0, y_0). The type of excitable behavior epitomized by the FN model is called type II [1] and is characterized by destabilization of the stationary state via Hopf bifurcation. The variable x is called the fast variable (due to $\epsilon \ll 1$) and corresponds to the membrane electrical potential. The variable y is the slow recovery variable and has no direct interpretation.

Each of $i = 1, 2 \ldots N$ units in (1) is coupled with each other unit and with itself. There are two major types of inter-neuronal couplings: the chemical and the electrical synapses. Time-delay τ is important, especially in the first type of synapses, but also plays an important role in the electrical junctions and in the transmission of an impulse through the dendrite. In (1) we use the electrical coupling with a time-lag and strength that is equal for all pairs of neurons.

The terms $\sqrt{2D}\mathrm{d}W_i$ represent stochastic increments of independent Wiener processes, i.e. $\mathrm{d}W_i$ satisfy

$$E(\mathrm{d}W_i) = 0, \qquad E(\mathrm{d}W_i \mathrm{d}W_j) = \delta_{i,j}\mathrm{d}t, \tag{3}$$

where $E()$ denotes the expectation over many realizations of the stochastic process.

Mean field approximation

In order to derive the approximate dynamical equations for the mean fields

$$X(t) = \frac{1}{N}\sum_{i}^{N} x_i(t) \equiv \langle x_i(t)\rangle, \qquad Y(t) = \frac{1}{N}\sum_{i}^{N} y_i(t) \equiv \langle y_i(t)\rangle \tag{4}$$

of the system (1) to be used in this paper we shall first suppose that: (a) The dynamics is such that the distributions of x_i and y_i are Gaussian and (b) for large N the average over N local random variables is given by the expectation with respect to the corresponding distribution, i.e. for example $\frac{1}{N}\sum_i^N x_i \approx E(x_i)$, where $E(x_i)$ is the expectation with respect to the distribution of $x_i(t)$. In the limit $N \to \infty$ the last assumption is expected to become an equality, implied by the strong law of large numbers [23]. In the mean field approach it is commonly assumed that (b) is approximately true even for finite but large N despite the nonzero interaction between the local random variables. The first assumption should be expected to be true when the noise intensity is small, i.e. $D \ll 1$ (see for example Refs. [19,20]). With these assumptions the system (1) of 2N SDDE can be reduced to five DDDE for the macroscopic variables $X(t), Y(t)$ and the second order cumulants. Further assumptions concerning the time scales of first and second order cumulants enables us to derive the final approximate system of only two DDDE.

The mean field assumption guarantees that global averages, like $(1/N)\sum_i^N x_i$, of local quantities are equal to the expectations with respect to distribution of the corresponding variable $E(x_i)$. Besides the mean values $X(t), Y(t)$ we introduce deviations from the expectations: $n_{x_i}(t) = X(t) - x_i(t)$, $n_{y_i}(t) = y_i(t) - Y(t)$. Because of the assumed Gauss distribution of each variable the first and the second order cumulants of these deviations are equal to the first and second order moments (i.e. to the first and second order centered moments of the variables x_i, etc). Furthermore, due to the same Gaussian assumption higher order cumulants are equal to zero, and this enables us to terminate the cumulant expansion of the dynamical equations. Details of the derivation are given in the Appendix. The result is a system of five deterministic delay-differential equations for the global variables and global centered moments:

$$s_x = \langle n_{x_i}^2(t)\rangle,\, s_y = \langle n_{y_i}^2(t)\rangle,\, u = \langle n_x n_y\rangle. \tag{5}$$

The equations are

$$\begin{aligned}
\epsilon\frac{\mathrm{d}X(t)}{\mathrm{d}t} &= X(t) - X(t)^3/3 - s_x(t)X(t) - Y(t) + c(X(t-\tau) - X(t)),\\
\frac{\mathrm{d}Y(t)}{\mathrm{d}t} &= X(t) + b,\\
\frac{\epsilon}{2}\frac{\mathrm{d}s_x(t)}{\mathrm{d}t} &= s_x(t)(1 - X(t)^2 - s_x(t) - c) - u(t)\\
\frac{1}{2}\frac{\mathrm{d}s_y(t)}{\mathrm{d}t} &= u(t) + D,\\
\frac{\mathrm{d}u(t)}{\mathrm{d}t} &= \frac{u(t)}{\epsilon}(1 - X(t)^2 - s_x(t) - c) - \frac{1}{\epsilon}s_y(t) + s_x(t).
\end{aligned} \tag{6}$$

The analogous set of ordinary differential equations was used to study the mean field approximation of the stochastic system of N neurons without delay in [7]. Eqs. (6) are delay-differential equations because the original system of stochastic equation (1) contains time-delay.

In order to further simplify the approximate system we shall suppose that relaxation time-scale of the second order moments is much faster then those of the first order moments. Thus we can replace in Eq. (6) the stationary values of s_x, s_y and u obtained by setting the right hand sides of the last three equations in (6) equal to zero. As the results we obtain the following two DDDE:

$$\begin{aligned}
\epsilon\frac{\mathrm{d}X(t)}{\mathrm{d}t} &= X(t) - X(t)^3/3 - \frac{X(t)}{2}\left[1 - c - X(t)^2 + \sqrt{(c - 1 + X^2(t))^2 + 4D}\right] - Y(t) + c(X(t-\tau) - X(t)),\\
\frac{\mathrm{d}Y(t)}{\mathrm{d}t} &= X(t) + b.
\end{aligned} \tag{7}$$

3. Stability and bifurcations of the stationary state

Stationary states, their stability and local bifurcations of the approximate system of DDDE (7) are determined by the standard procedure. It is remarkable that such a crude approximation provides relevant information about the exact system.

There is only one stationary state of (7) given by:

$$X(t) \equiv X_0 = -b, \qquad Y(t) \equiv Y_0 = \frac{-b}{2}\left[1 + b^2/3 + c - (4D + (c + b^2 - 1)^2)^{1/2}\right]. \tag{8}$$

Local stability of (8) is determined from the roots of the characteristic equation. Due to the time-delay the system (7) has an infinite-dimensional state space, and the characteristic equation is transcendental with an infinite number of roots. The characteristic equation is

$$\lambda^2 - \frac{1}{2\epsilon}\left[1 - c + b^2 - (m^2 + 4D)^{1/2} - \frac{2b^2 m}{(m^2 + 4D)^{1/2}}\right]\lambda + \frac{1}{\epsilon} - \frac{c}{\epsilon}\lambda\exp(-\lambda\tau) = 0, \tag{9}$$

where $m = c - 1 + b^2$.

Bifurcations of the stationary state occur for those values of the parameters such that any of the infinite number of roots of (9) has the real part equal to zero [24]. This is possible only if $\lambda = \mathrm{i}\omega$, where ω can be taken to be positive. Substitution of $\lambda = \mathrm{i}\omega$ in (9) gives

$$\sqrt{2}\omega_\pm = \left[(-k^2 + c^2/\epsilon^2 + 2/\epsilon \pm (k^2 - c^2/\epsilon^2 - 2/\epsilon)^2 - 4/\epsilon^2)^{1/2}\right]^{1/2}, \tag{10}$$

where

$$k = \frac{1}{2\epsilon}\left[1 - c + b^2 - (m^2 + 4D)^{1/2} - \frac{2b^2 m}{(m^2 + 4D)^{1/2}}\right].$$

Equating the real and the imaginary parts of the left hand side of (9) (with $\lambda = \mathrm{i}\omega$) with zero, and after substitution of (10) gives critical values of the time-lag τ expressed in terms of other parameters c, D and b. The expressions read: if

$$\frac{-\omega_\pm^2 + 1/\epsilon}{c\omega_\pm/\epsilon} \geq 0 \tag{11}$$

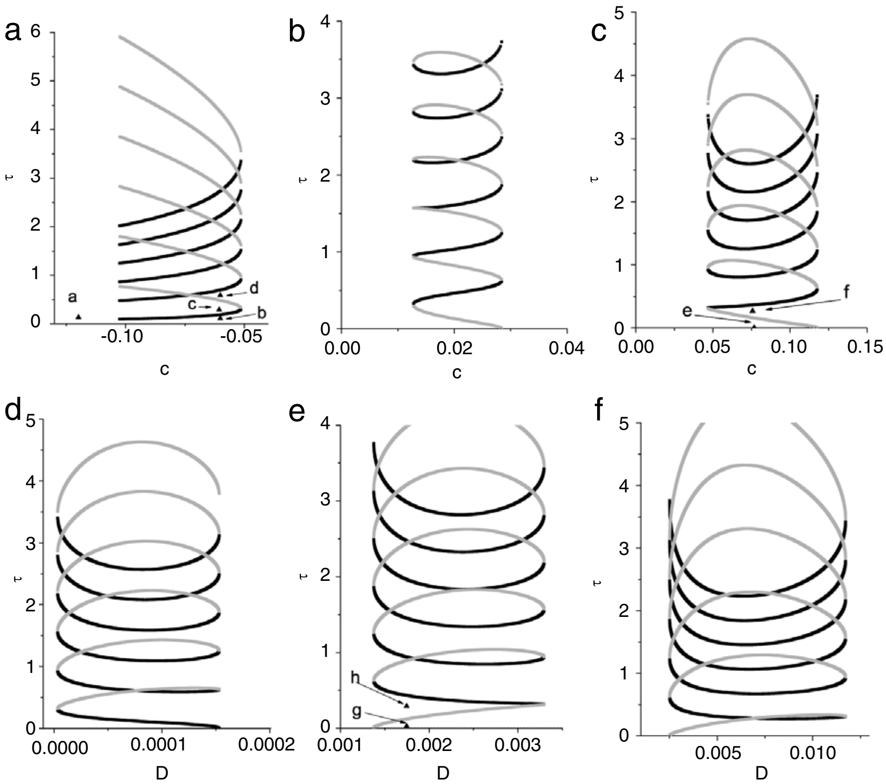

Fig. 1. Bifurcation curves $(\tau^j_{c,\pm}, c)$ (a, b, c) for fixed $D = 0$ (a), $D = 0.001$ (b), $D = 0.003$ (c) and $(\tau^j_{c,\pm}, D)$ (d, e, f) for fixed $c = -0.05$ (d), $c = 0.05$ (e), $c = 0.1$ (f). In all figures $b = 1.05$. Gray curves correspond to $\tau^j_{c,-}$ and black curves to $\tau^j_{c,+}$, for $j = 0, 1, 2, 3, 4, 5$.

then

$$\tau^j_{c,\pm} = \left[\cos^{-1}(-k\epsilon/c) + 2j\pi\right]/\omega_\pm, \quad j = 0, 1, 2 \dots \tag{12}$$

and if (11) is not satisfied then

$$\tau^j_{c,\pm} = \left[-\cos^{-1}(-k\epsilon/c) + (2j+2)\pi\right]/\omega_\pm, \quad j = 0, 1, 2 \dots. \tag{13}$$

It can be shown by direct substitution that

$$\left(\frac{\mathrm{d}\Re\lambda}{\mathrm{d}\tau}\right)_{\tau=\tau_{c,+}} > 0, \qquad \left(\frac{\mathrm{d}\Re\lambda}{\mathrm{d}\tau}\right)_{\tau=\tau_{c,-}} < 0, \tag{14}$$

so that on the bifurcation curves $\tau^j_{c,+}$ or $\tau^j_{c,-}$ one unstable direction is created or destroyed. Together with the stability properties for $\tau = 0$ the bifurcation curves (12), (13) and (10) completely solve the problem of stability of the stationary state. It can be shown by rather lengthy calculations that the bifurcations for $\tau^j_{c,\pm}$ are the Hopf supercritical or subcritical bifurcations of the DDDE (7).

Bifurcation curves $\tau^j_{c,\pm}(c)$ for fixed $D, b = 1.05$ and $\tau^j_{c,\pm}(D)$ for fixed $c, b = 1.05$ are illustrated in Fig. 1 for different values of D (Fig. 1a, b, c) and c (Fig. 1d, e, f). The value $b = 1.05$ renders the stationary state X_0, Y_0 stable and excitable when $\tau = 0$ and $D = 0$.

The predictions given by the bifurcation values (11) and (13) of the system (7) are checked against the numerical solutions of the exact system (1). To check the approximate predictions of the bifurcations of stability for the noisy system, i.e. when $D \neq 0$, a proper notion of stochastic bifurcations would be necessary [23]. Instead we use the sample paths of the SDDE (1) with large N and for $D \neq 0$ to illustrate that these paths remain in the vicinity of the stationary solution if the approximate system's stationary state is stable, or near a periodic solution when the state of the approximate system is unstable. Fig. 2 presents enlarged parts of bifurcation diagrams in Fig. 1, where particular values of the parameters that correspond either to stable or to unstable stationary states of (7) are indicated. These parameter values are replaced in the original system (1) with large N and particular sample paths of (1) with these parameter values are computed numerically. Time series of the global variable $X(t)$ along such sample paths are shown in Fig. 3, for the system (1) with $N = 95$. There is nothing special with $N = 95$ and the same qualitative behavior of $X(t)$, $Y(t)$ is obtained for any moderately large N. It is clear that when the

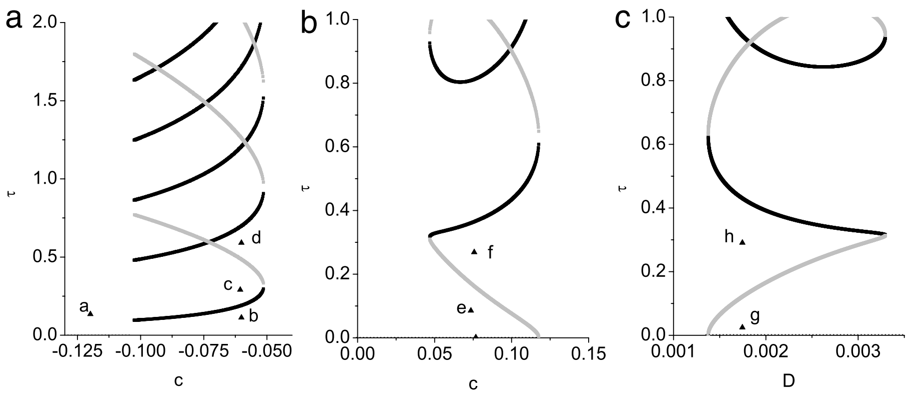

Fig. 2. Enlarged parts of bifurcation diagrams presented in Fig. 1a, c, e with parameter values, indicated by letters: a, b, c, d (fig. a), e, f (fig. c), g, h (fig. e), that are used for comparison with the exact system presented in Fig. 3.

bifurcation diagrams of the approximate system (7), illustrated in Figs. 1 and 2, predict that the stationary solution is stable (like in the cases: b, d, f, h in Fig. 2) the sample paths of the exact system display small stochastic fluctuations around the stationary state. Otherwise, when the stationary state of (7) is unstable, as indicated in the bifurcation diagrams (parameter values corresponding to the points a, c, e, g in Fig. 2) the sample paths of the exact system displays coherent oscillations with large amplitude, indicating that the exact system has a stochastically stable periodic solution. The quantitative agreement between the domains of stability in the parameter (D, c, τ) space of the approximate system (7) and the exact system (1) is indeed quite remarkable. It should be expected that such an agrement should be observed for small values of D since this is one of the conditions which guarantees that the local random variables have a Gaussian distribution, which is one of the assumptions in the derivation of the mean field equations. It is interesting to observe the domains of the time-lag where the bifurcation diagrams in Figs. 1 and 2 predict that the non-zero time-lag induces stabilization of the stationary state. This secession of oscillations due to the specific non-zero interval of the time-lag values is correctly predicted for the global variables of the exact system. The same phenomenon, known by the name of oscillation death due to time-delay, has been observed in other systems with time-delay induced Hopf bifurcation see for example Ref. [2] and the references therein).

It should be stressed that the agreement in the predictions of the approximate system and the large exact system goes only as far as the parameter domains of stability are considered. It should be expected that the predictions of the parameter stability domains based on (7) should well approximate the parameter stability domains of the exact system for small values of D since this is one of the basic assumptions in the derivation of the mean field equations. Also, the interaction strength c should be relatively small in order for the mean field assumption to be valid for moderately large (but finite) N. However, this domain of small values of c includes relevant bifurcations of the stationary state predicted by (7) and occurring in (1). Furthermore, large values of τ induce an unstable stationary state and stable oscillatory behavior in both systems (7) and (1) so formally there is no restriction on the time-lag τ as far as we are interested only in the stability of the stationary state.

The assumption of small D and c, which are crucial in the derivation of the approximate model (7) imply that the approximate model is useful only for the analyses of the stability of the stationary state and the dynamics for parameter values near the bifurcation values. It is not expected that the approximate model can capture the qualitative properties of the exact dynamics for large noise or strong coupling and far away from the equilibrium.

Nevertheless we would like to point out that the approximate simple system (7) can be used to successfully predict the average frequency of spiking of the exact system, again for small D and c. The exact system in the oscillatory regime produces a sequence of stochastically distributed spikes of the collective variable $X(t)$. For larger time-lags, when the time-lag induced oscillations dominate the noisy fluctuations, the oscillatory dynamics is more regular and is characterized by a well defined frequency. In any case, the averaged frequency of spiking, that is the number of spikes of $X(t)$ in a sufficiently long interval of time divided by this time interval, is an important characteristic of the spiking sequence. This averaged frequency is well predicted by the exact frequency of the approximate systems for the same values of the parameters, especially when the oscillatory dynamics dominates stochastic fluctuations, i.e. for larger time-lags, as is illustrated in Fig. 4. The time-lag in Fig. 4 is $\tau = 2.8$, much larger than the time-lags on Fig. 3, which have been chosen to illustrate the influence of the bifurcations for the smallest critical $\tau_{c,\pm}$. For such small values of τ the sequence of spikes of $X(t)$, which occur if τ is in one of the intervals predicted by the low lying bifurcation curves of the approximate system (7), is quite irregular as is seen in Fig. 3g. In this case, large portions of the time series, or many sample paths, have to be included in the computation of the average frequency, but nevertheless the average frequency is well predicted by the approximate system. Of course, in this case the stochastic sequence of $X(t)$ along the sample paths of the exact systems are not approximated by the deterministic orbit of the approximate model.

It should be made clear that it is not to be expected that the values of X and Y for the deterministic approximate system (7) should reproduce stochastic orbits $X(t)$, $Y(t)$ for the large exact system or their ensemble averages. The correspondence

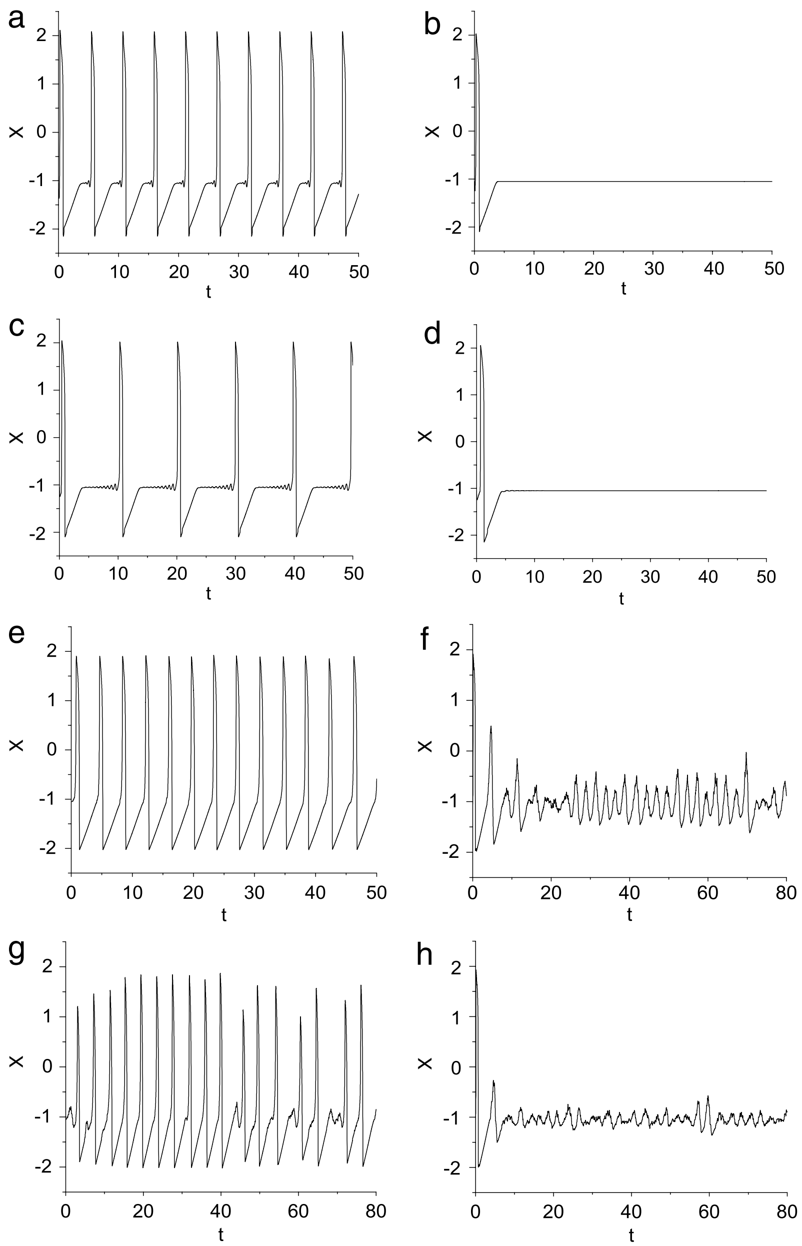

Fig. 3. Illustrates dynamics of the global variable $X(t)$ for the exact system of $N = 95$ units for parameter values corresponding to the stable or unstable state of the approximate system (7). Parameter values corresponding to a, b, c, d, e, f, g, h, indicated in Fig. 2, are (a) $(c, \tau) = (-0.12, 0.14)$; (b) $(-0.06, 0.11)$, (c) $(-0.06, 0.29)$, (d) $(-0.06, 0.59)$, (e) $(0.07, 0.09)$, (f) $(0.08, 0.27)$, (g) $(D, \tau) = (0.002, 0.02)$, (h) $(0.002, 0.29)$.

between the orbits of the two systems for the same values of the parameters in different domains is only qualitative in the sense that they share the same types of attractors.

4. Summary

We have studied validity of the mean field approximation for the treatment of stability and bifurcations of the stationary state of a large collection of FitzHugh–Nagumo excitable neurons with noise and all-to-all coupling with delays, modelled by $N \gg 1$ stochastic delay-differential equations. Standard assumptions of the mean field approach are used to derive the system of only two deterministic delay-differential equations. The stability and bifurcations of the stationary state of the approximate system can be studied analytically. The bifurcation curves of the approximate system give relevant information about the global variables of the exact large system. For zero and sufficiently small noise there is remarkable quantitative agreement of the parameter bifurcation values. Otherwise, it should not be expected that the approximation

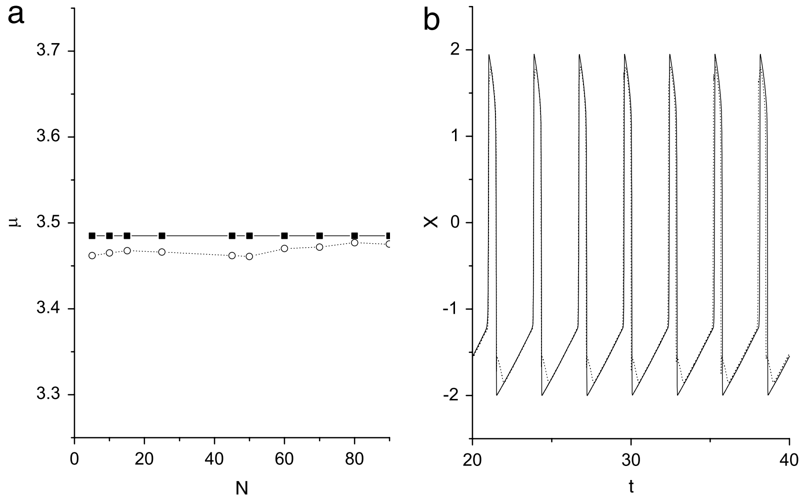

Fig. 4. (a) Illustrates average frequency of the exact system (solid line, boxes) and the exact frequency of the approximate system (7) (dotted line, circles) for the same values of the parameters: $\tau = 2.8$, $D = 0.003$, $c = 0.1$; (b) illustrates segments of the time series of approximate (dotted) and exact (full) $X(t)$ values for the parameters as in (a) and $N = 60$.

gives applicable results when the noise is too large, primarily because the assumption about the Gaussian distribution of values of the dynamical variables is not valid for large noise.

Using the approximate system it is predicted, and confirmed by direct numerical simulations on the large exact system, that the time-lag in a non-zero interval can stabilize the global variables onto the stationary values even when for zero time-lag the global variables perform large oscillations. This is reminiscent of the phenomenon of the oscillation's death due to the time-delay, although in this case the relevant dynamics is that of the averaged global variables and not that of the individual neurons.

We have derived the mean field approximation for the delayed coupled noisy system using the example of FitzHugh–Nagumo neurons in the excitable regime. It is expected that the approximations are equally valid for noisy delayed coupled type I excitable systems like the Terman–Wang neurons, or for bursting neurons like the Hindmarsh–Rose model. Also the approximation should be applicable under the same assumptions for neurons interacting by delayed chemical rather than electrical coupling.

Acknowledgement

This work is partly supported by the Serbian Ministry of Science contract No. 141003.

Appendix

The system of Eqs. (1) and (2) can be written in the form:

$$\epsilon \mathrm{d}x_i = (x_i - x_i^3/3 - y_i + I)\mathrm{d}t + c(\langle x(t-\tau)\rangle - x_i)\mathrm{d}t$$
$$\mathrm{d}y_i = (x_i + b)\mathrm{d}t + \sqrt{2D}\mathrm{d}W_i$$

where:

$$\langle x(t-\tau)\rangle = \frac{1}{N}\sum_i (x_i(t-\tau)).$$

The bracket $\langle x\rangle$ is always used to denote the average over the N units of the local variable x_i, which is, by the mean field assumption, for large N, approximately equal to the average over the assumed Gauss distribution of the corresponding local variable x_i.

Next we introduce deviations from the mean field:

$$n_{x_i}(t) = \langle x(t)\rangle - x_i(t), \qquad n_{y_i}(t) = \langle y(t)\rangle - y_i(t).$$

Deviations will always appear averaged over N, i.e. in the form of $\langle n_x\rangle$ and $\langle n_y\rangle$, so that the index i is in fact redundant. Correlations between centered moments are defined as

$$s_x(t) = \langle n_x^2\rangle, \qquad s_y(t) = \langle n_y^2\rangle, \qquad u(t) = \langle n_x n_y\rangle.$$

Our goal is to derive the equations governing the evolution of the averages: $X = \langle x \rangle$, $Y = \langle y \rangle$, s_x, s_y, u. Due to the mean field assumption, these averages can be computed as averages over the stochastic distributions of the local quantities, which are by assumption Gaussian. The equation for the derivatives of $X = \langle x \rangle$, $Y = \langle y \rangle$, s_x, s_y, u will contain averages of monomials in local variables of various orders. In order to handle these we shall need to use the formulas for the cumulant expansions up to the fourth order in the local quantities. The general formulas for the cumulant expansion can be found for example in Ref. [25]. Due to the assumed Gaussian distribution the third and the fourth order cumulants (and all of the higher order) are equal to zero, which will be used to express averages of the monomial in the local variables that appear in the evolution equations.

Using the cumulant formulas one computes the following expressions which will be used to obtain the evolution equations:

From the cumulant $\langle\langle x^2 y \rangle\rangle = 0$ it follows that

$$\langle x_i^2 y_i \rangle = Y s_x + Y X^2 + 2Xu.$$

From the cumulant $\langle\langle x^3 y \rangle\rangle = 0$ it follows that

$$\langle x_i^3 y_i \rangle = 3 s_x u + 3X^2 u + Y X^3 + 3XY s_x.$$

Similarly one obtains:

$$\begin{aligned}
&\langle x_i^2 \rangle = s_x + X^2, \\
&\langle x_i^3 \rangle = X^3 + 3X s_x, \\
&\langle x_i^4 \rangle = X^4 + 6X^2 s_x + 3 s_x^2, \\
&\langle x_i y_i \rangle = U + XY. \qquad (15)
\end{aligned}$$

These expressions provide the necessary ingredients to obtain the equations (6).

Taking the average of the equations for $\dot{x}$ and $\dot{y}$ gives the first two equations of the system (6). Next consider the equation for $\dot{s}_x$.

$$\begin{aligned}
\dot{s}_x &= 2\langle X(t)\dot{X}(t) - X(t)\dot{x}_i(t) - x_i(t)\dot{X}(t) + x_i(t)\dot{x}_i(t)\rangle \\
&= -2\frac{X(t)}{\epsilon}[X(t) - X(t)^3/3 - X(t)s_x(t) - Y(t) + c(X(t-\tau) - X(t))] \\
&\quad + \frac{2}{\epsilon}\langle x_i(t)^2 - x_i(t)^4/3 - x_i(t)y_i(t) + c x_i(t)X(t-\tau) - c x_i(t)^2\rangle \\
&= \frac{2}{\epsilon}[-X^2(t)s_x(t) + s_x(t) - s_x^2(t) - u(t) - c s_x(y)] \qquad (16)
\end{aligned}$$

which is the third equation (6). In the last equality we used the expressions obtained from the cumulant formulas.

The equation for $\dot{s}_y$ is obtained as follows:

$$\dot{s}_y = \mathrm{d}\langle Y(t)^2 - 2Y(t)y_i(t) + y_i(t)^2\rangle/\mathrm{d}t = -2Y(t)\dot{Y}(t) - \mathrm{d}\langle y_i(t)\rangle/\mathrm{d}t.$$

Using the Ito chain rule this becomes:

$$\begin{aligned}
&-2Y(t)[X(t) + b] + \langle 2y(t)\mathrm{d}y_i(t)/\mathrm{d}t + 2D\rangle \\
&\quad = -2Y(t)X(t) - 2Y(t)b + \langle 2y_i(t)x_i(t) + 2y_i(t)b + 2y_i(t)\sqrt{2D}\mathrm{d}W_i + 2D\rangle \\
&\quad = -2Y(t)X(t) - 2Y(t)b + 2u(t) + 2X(t)Y(t) + 2Y(t)b + 2D \\
&\quad = 2u(t) + 2D, \qquad (17)
\end{aligned}$$

which is the fourth equation (6).

Similar calculations result in the $\dot{u}$ equation (6).

$$\begin{aligned}
\dot{u}(t) &= \mathrm{d}\langle X(t)Y(t) - X(t)y_i(t) - Y(t)x_i(t) + x_i(t)y_i(t)\rangle/\mathrm{d}t \\
&= -X(t)\dot{X}(t) - Y(t)\dot{X}(t) + \langle y_i(t)\dot{x}_i(t)\rangle + \langle \dot{y}_i(t)x_i(t)\rangle = \cdots \\
&= \frac{1}{\epsilon}u(t)[1 - X^2(t) - s_x(t) - c] - \frac{1}{\epsilon}s_y(t) + s_x(t). \qquad (18)
\end{aligned}$$

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